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Descriptive epidemiology of *Heligmosomoides polygyrus* in *Apodemus sylvaticus* from three contrasting habitats in south-east England

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Abstract

Seasonal fluctuations in the prevalence and intensity of infection with *Heligmosomoides polygyrus* (Nematoda) were studied in *Apodemus sylvaticus* (wood mouse, $n = 399$), sampled from three contrasting habitats in southern England, to test the hypothesis that both intrinsic (host sex, age) and extrinsic (season, site) factors influence parasite burdens. Maximum likelihood techniques based on log linear analysis of contingency tables were employed to generate a minimum sufficient model for prevalence of infection and 3-way ANOVA with negative binomial errors was used to evaluate the relative contribution of the principal factors and their interactions in explaining variation in worm burdens. Host age could not be entered into either statistical model because of some incomplete subsets of data. However, it was evident that in general juvenile mice carried lower worm burdens compared with adults, although these increased towards the winter season. Host sex was not a significant factor, other than in making a contribution to a weak significant interaction between sex and site, arising from male bias in one site and female bias in the remaining two. The principal determinants of variation in worm burden were the extrinsic factors, site and season, with an approximately equal weighting, and their interaction. These effects arose because worm burdens were lower at Dungeness and showed quite different seasonal patterns to the Egham and Isle of Wight sites. We propose that the unique character of the Dungeness habitat was not conducive to optimal transmission of *H. polygyrus* throughout most of the year (excepting spring) and we suggest possible explanations for these observations.

Introduction

The helminth fauna of British rodents is well documented from a variety of different study sites across the region. Among the more common species of the wood mouse (long-tailed field mouse) *Apodemus sylvaticus* is the trichostrongyloid nematode *Heligmosomoides polygyrus polygyrus* which has been detected in most wood mouse populations, generally occurring in some 80% of the host population, and often reported as universal (100%) in the population (Lewis, 1968). Sites where it appears to be unusually rare have also been documented (Clandeboye Estate in Co. Down, N. Ireland, Montgomery & Montgomery, 1988).

Seasonal fluctuations in adult worm burdens are well

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established (Elton *et al.*, 1931), these generally showing a peak in the late winter–spring–early summer period before the influx of young mice into the sampled populations. The appearance of young, uninfected animals results in a dilution effect, and this together with the gradual loss of older worms, acquired in the preceding year, from senility and immunity, underlies the fall in the overall mean worm burden by late summer (Montgomery & Montgomery, 1988; Gregory, 1992). By the winter months the young animals will have picked up infection and worm burdens increased in the population. *Heligmosomoides polygyrus* is a long-lived parasite, single-pulse experimental infections of the wild strain in its natural host surviving for 3–4 months (Gregory *et al.*, 1990). In the UK, excepting short unusually cold spells, transmission probably occurs across most of the winter period because of the generally mild weather, so that by spring–early summer 100% of the over-wintering host population can be expected to carry worms (Montgomery & Montgomery, 1988). Nevertheless, the precise timing of the peak infections has varied between studies, presumably reflecting differences in local climatic and environmental factors and/or in host behaviour/community composition (O'Sullivan *et al.*, 1984).

The majority of surveys also report heavier infections in male wood mice compared with females (Lewis, 1968; Lewis & Twigg, 1972), although not all such surveys have detected significant sex differences in worm burden (Gregory, 1992; Sharpe, 1964). Another important factor is age. Being a long-lived parasite and one which elicits only weak immunity in its host, worm burdens accumulate with time, as animals grow and become heavier (Elton *et al.*, 1931; Gregory, 1992; Gregory *et al.*, 1992). Some reports have shown that in a subset comprising the older animals (especially females) worm burdens may decline (Elton *et al.*, 1931), probably as a consequence of immune mediated rejection of established parasites and resistance to further larval invasion (Gregory, 1992).

The ecology of the local habitat, with variation in the quality/quantity of available food resources, has also been suggested as playing a key role in influencing the parasite burdens of specific mouse communities, (Montgomery & Montgomery, 1990). This may explain some of the differences between the findings from surveys conducted in different parts of the country with respect to such features as presence/absence of a sex difference, high vs. low overall worm burdens, temporal differences in seasonal peaks of infections, etc. However, with the exception of the studies by Montgomery & Montgomery (1988, 1989) from N. Ireland, there are no UK based studies, where mice from several disparate sites, differing in habitat quality, have been compared across the same succession of seasons, so that the importance of site of capture (habitat) can be assessed, in relation to the known alternative variables affecting parasite burden, by rigorous statistical analysis.

In this paper, we report a study which tested the hypothesis that in addition to intrinsic factors (host sex and age), extrinsic factors (season and site of capture) play a major role in determining parasite burdens. In particular, we predicted that habitat type would have a marked effect on the transmission. As a reference point we selected one of the habitats which has already been studied in some detail, the Egham site surrounding Royal Holloway (Lewis & Twigg, 1972). The second site was an agricultural region on the Isle of Wight and the third the comparatively harsh, and more open Dungeness wetland area, selected on the basis of its unique vegetation and the presence of an acidic soil. We report here that the main effect of site on prevalence and intensity of infection with *H. polygyrus* was of the same order as that of the well documented pronounced seasonal effect.

Materials and methods

Study sites

Dungeness

Dungeness is situated in Kent (Grid reference, 074183) and composed of flint shingle derived from the Sussex Cliffs. The best examples of the shingle wetlands remaining today are Open Pits 1 and 2 situated on Denge Beach completely separated by shingle (Ferry & Waters, 1988). These are the largest and youngest pits, still containing standing open water despite some marginal drying out. Approximate areas, including the marginal vegetation are 5.4 ha for Open Pit 1 and 3.8 ha for Open Pit 2. The existing flora of these pits has been comprehensively surveyed and simplified by describing three main vegetational zones: neutral reedswamp (mainly *Phragmites australis* and *Schoenoplectus tabernaemontani*), oligotrophic/acidic/deep-deposit areas and a marginal wetland fringe with little underlying organic material. The dried-out sedge marsh of the open pits, which was considered to be representative of the typical habitat in Dungeness, was used as the principal collecting area for mice.

Egham

Mice were collected from part of the grounds of Royal Holloway, University of London, Egham, Surrey (Grid reference, 993693). This area consists of 5 ha of deciduous woodland. Sycamore (*Acer pseudoplatanus*), gorse (*Ulex europaeus*) and holly (*Ilex aquifolium*) form a series of copses with a ground flora of grass, comprising the tufted hair grass (*Deschampsia caespitosa*) and meadow grass (*Poa annua*). The ground cover was mainly bracken, bramble, fallen timber and rotting tree stumps. It also comprises an old larch (*Larix decidua*) plantation with a hard wood fringe which leads into an extensive area of oak (*Quercus robur*) woodland, this providing a good habitat for wood mice.

Isle of Wight

The collecting site on the Isle of Wight consisted of approximately 10 ha of farm land interspersed with copses and larger areas of woodland (Grid reference, 523882). The ground was covered with grass, the dominant species being the bent grass (*Agrostis tenuis*) and couch grass (*Agropyron repens*). The farm was surrounded by planted hedgerows of conifers, rhododendron and deciduous trees where most of the mice were caught. The natural deciduous trees of this part are the hornbeam (*Carpinus betulus*), horse chestnut (*Aesculus hippocastanum*) and sycamore (*Acer pseudoplatanus*).

Collection of mice and parasites

Trapping was carried out for 3 days at 2-month intervals from October 1991 to August 1992 using Longworth traps provided with hay and food. One hundred Longworth traps were used each night and their positions recorded on a local map.

Mice were retrieved from traps and killed by exposure to a piece of chloroform-soaked cotton wool. For each mouse examined, the date of trapping, locality, body length (head and the body), and sex were noted. For analysis, mice were separated into two age groups, juveniles and adults, as previously described by Lewis (1968) and Corbet & Harris (1991). The alimentary canal was then removed for further examination and the eviscerated body weight of each animal was recorded. The small intestine from pyloric sphincter to caecum was separated from the surrounding fat tissue and placed in a Petri dish containing physiological saline. The small intestine was opened longitudinally and examined for helminth parasites under a low power binocular microscope. The parasites were carefully removed, identified, sexed and counted. The prevalence (percentage of mice infected in each subset), mean intensity of infection (including uninfected mice in each subset) and the frequency distribution of *H. polygyrus* were then calculated. The moment estimate of the negative binomial exponent k was calculated from the equation:

$$p = 1 - [1 + m/k]^{-k}$$

where p = prevalence and m = mean intensity.

Statistical analysis

The results are presented as prevalence of infection and the mean intensity of infection (= mean worm burden of each subset, **including uninfected animals**, ± standard error of the mean). The total data comprises 4 factors (site, season, sex and age) and 2 variables (prevalence & number of worms). However, age (juvenile vs. adult) presented problems in analysis because data were totally missing from some subsets, resulting in empty cells in multiway contingency tables (table 1, no male mice were caught in spring from Dungeness, neither male nor female juvenile mice were examined from the Isle of Wight in spring and no male juveniles in winter) or was represented by a single animal (male juvenile from Egham in winter, female juvenile from the Isle of Wight in winter). For this reason, the statistical analysis was conducted only on the data from adult animals and hence restricted to the effect of 3 factors (site, sex and season). The significance was set at $P \leq 0.05$.

Prevalence was analysed by maximum likelihood techniques based on log linear analysis of contingency tables implementing the software package, Statgraphics Version 7. Beginning with the most complex model, involving all possible main effects and interactions, those combinations which did not contribute significantly to explaining variation in the data were eliminated stepwise beginning with the least significant. A minimum sufficient model was then obtained, for which the likelihood ratio of Chi squared was not significant, indicating that the model was sufficient in explaining the data.

Worm burdens were analysed by GLIM (General Linear Models) using a model with negative binomial errors as reported previously (Crawley, 1993; Behnke *et al.*, 1994; Wilson & Grenfell, 1997). We began with the full factorial model involving all possible main effects and interactions and deleted combinations stepwise, commencing with the most complex (the 3 way interaction) until only the main effects remained. At each step (subtraction of the relevant term) the change in model deviance was noted and used to calculate Chi squared (change in deviance/ scale parameter) and thereby the significance of its contribution to the overall model. The main effects were analysed in turn but each was replaced in the model before evaluation of the remainder. The model was then re-run, including only those combinations which had shown significance (minimum sufficient model), to locate the level at which significant variation resided within factors.

Results

Apodemus sylvaticus

A total of 399 *A. sylvaticus*, 210 male and 189 female, was trapped from the three sites as summarized in table 1. Most of the mice were caught at Dungeness and the fewest at the Isle of Wight site. Across all three sites and among adult animals, more males than females were examined. This difference was significant (the minimum sufficient maximum likelihood model, described below, incorporated sex of host) but no significance emerged in the number of adults sampled by season nor by site. It was not possible to analyse the significance of juvenile numbers in the statistical model because there were too many empty cells, but 40.4% of the total sample ($n = 161$, 55 males and 106 females) were classed as juveniles.

Prevalence of H. polygyrus

Overall, 302 mice (75.6%) were infected with *H. polygyrus* and 97 mice (24.3%) were uninfected. Of these, 168 male (80%) and 134 female (70.9%) mice carried worms. The summary statistics by site of capture and host sex are given in table 2 and the complete data (by site, age, season and sex) are illustrated in fig. 1.

We analysed further the importance of the three factors, site (3 levels), season (4 levels) and sex (2 levels) in affecting the number of adult animals carrying the parasite, omitting age because of missing data from some sites at specific times of the year. The minimum sufficient model was found to incorporate the following combinations: site × infection interaction, season × infection interaction, and sex of mice (the likelihood ratio of χ^2 was 38.00 with 35 df, $P = 0.334$).

Thus among the adult mice there were significantly more males ($n = 155$) than females ($n = 83$) (table 1). There was also a significant effect of season on the prevalence of infection (season × infection interaction), as can be seen from the Dungeness data where there was a clear reduction in prevalence among adult mice in summer and autumn (fig. 1B). A similar although less marked drop was also evident at Egham (fig. 1D). There was no variation in prevalence at the Isle of Wight site (fig. 1F) where the percentage of adult mice carrying worms was

Table 1. Numbers of *Apodemus sylvaticus* examined by site, sex, age and season.

Site	Sex	Age	Season				Total by subset	Total by site
			Spring	Summer	Autumn	Winter		
Dungeness	Male	Juvenile	0	17	13	2	32	
		Adult	19	22	9	7	57	
								185
	Female	Juvenile	4	18	28	8	58	
		Adult	4	13	15	6	38	
Egham	Male	Juvenile	4	5	4	1	14	
		Adult	17	20	7	12	56	
								133
	Female	Juvenile	9	7	10	7	33	
		Adult	10	6	6	8	30	
Isle of Wight	Male	Juvenile	0	6	3	0	9	
		Adult	15	7	13	7	42	
								81
	Female	Juvenile	0	8	6	1	15	
		Adult	8	2	2	3	15	
Total by season			90	131	116	62	399	399

100% throughout the study, but the numbers of animals sampled from this site were lower than the other two sites. The site × infection interaction confirmed that the prevalence of infection differed significantly between the three sites.

The prevalence of infection among juvenile mice appeared to increase from spring through to the winter sampling period, although the data from the four females examined from Dungeness in spring was not consistent with this interpretation.

Intensity of infection with H. polygyrus

The mean worm burdens recovered from each subset of mice are summarized by site and host sex in table 2 and the complete data-set (by site, age, season and sex) is illustrated in fig. 2. As with prevalence, statistical models incorporating age proved difficult to interpret because of missing data subsets. We therefore confined the analysis to adult mice only. The full factorial model is summarized in table 3.

Of the three factors affecting variation in worm burden, host sex was the least important, with no significance associated with the main effect of sex, nor the sex × season interaction. However, host sex did contribute to the significant site × sex and the 3 way interaction. This is evident from fig. 2, where marginally higher mean worm burdens are shown among male compared with female mice from the Isle of Wight site (fig. 2F), but the pattern is reversed in three out of four seasons at Egham (fig. 2D) and all four seasons at Dungeness (fig. 2B).

Quite clearly there was a highly significant main effect of site and from fig, 2 it is apparent, despite the seasonal variation (the highly significant site × season interaction), that overall the intensity of infection was highest at the Isle of Wight site and lowest at Dungeness.

Table 2. Summary statistics for *Heligmosomoides polygyrus* infections in *Apodemus sylvaticus* by site and host sex (age and season condensed).

Site	No. of mice	Prevalence (%)	Mean intensity ± S.E.M	Variance	Range
Dungeness					
Male	89	65.2	7.8 ± 1.6	228.24	0–67
Female	96	54.2	4.0 ± 1.0	95.15	0–66
Egham					
Male	70	88.6	18.7 ± 2.8	555.45	0–111
Female	63	90.5	17.3 ± 2.7	444.63	0–105
Isle of Wight					
Male	51	94.1	32.8 ± 4.6	1068.50	0–126
Female	30	83.3	18.4 ± 3.9	454.81	0–63
All sites					
Male	210	80	17.5 ± 1.7	632.61	0–126
Female	189	70.9	10.7 ± 1.3	311.73	0–105

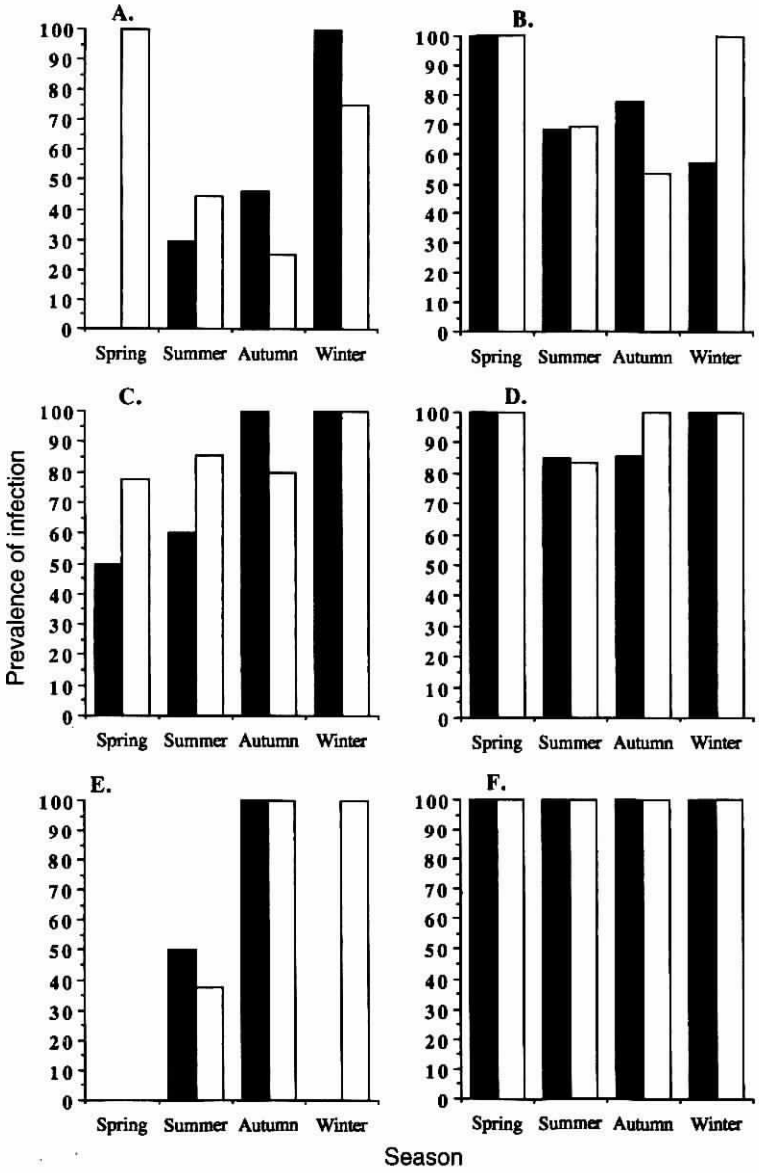

Fig. 1. Seasonal variation in the prevalence of infection with *Heligmosomoides p. polygyrus* in *Apodemus sylvaticus* across three habitats (A and B, Dungeness; C and D, Egham; E and F, Isle of Wight) and by host age (juveniles A, C and E; adults B, D and F) and host sex (males filled in columns, females open columns).

In each site there was also a significant seasonal effect, indicating annual fluctuations in parasite burden among adult mice, but the highly significant interaction showed that the seasonal pattern varied between the three sites. This can be clearly seen from fig. 2, where the general pattern at the Isle of Wight and Egham sites was for worm burdens to fall in summer to a low in the autumn, whereas at Dungeness the lower worm burdens lasted throughout the winter. The only season when higher worm burdens were detected at Dungeness was spring.

In comparison to the worm burdens harboured by adult mice, those encountered in juveniles were lower although we did not test this statistically. Given the absence of data for some subsets, particularly the Isle of Wight and Dungeness sites, the only pattern which loosely emerged out of the data in fig. 2A, C and E was a tendency for worm burdens to rise by winter at the Isle of Wight and Egham sites, whilst peaking later in the spring at Dungeness.

Frequency distribution of H. polygyrus

Adult *H. polygyrus* were typically over dispersed in the host population in the three sites (Dungeness $k = 0.27$, $S2/X = 27.6$, $\chi^2 = 5078.4$, $P < 0.0005$; Egham $k = 0.61$, $S2/X =$

Table 3. Statistical analysis of the factors affecting the intensity of infections with *Heligmosomoides polygyrus* in adult *Apodemus sylvaticus* by site, sex and season, through a 3-way ANOVA with negative binomial errors.

Source of variation	Change in deviance[1]	Degrees of freedom	Scale parameter	Scaled deviance*	*P*
Site	1256.0	2	24.97	50.300	<0.001
Season	1420.0	3	25.57	55.534	<0.001
Sex	0.884	1	19.67	0.045	NS
Sex × season	79.69	3	19.75	4.035	NS
Site × season	572.0	6	19.66	29.095	<0.001
Site × sex	157.2	2	17.62	8.922	<0.020
Site × season × sex	251.31	6	17.06	14.730	<0.025

The full model deviance was 3502.2 with a scale parameter of 16.37.
NS = Not significant.
1 = Change in deviance following the removal of the combination specified in 'source of variation' column from the full factorial model. We begin by removing the 3 way interaction from the model and progressively remove the combinations in the order from the base of the table towards the top. The main effects, however, were removed to assess the change in deviance but then replaced before proceeding further.
*, Scaled deviance is a measure of the contribution of the factor specified under the column labelled 'source of variation' to explaining the variation in the data. It is calculated by fitting an analysis of variance with negative binomial errors through GLIM and is distributed as χ^2.

27.7, $\chi^2 = 3656.4$, $P < 0.0005$; the Isle of Wight $k = 0.6$, $S2/X = 32.1$, $\chi^2 = 2564$, $P < 0.0005$).

Discussion

The study described in this paper focused on the contribution of two extrinsic (site and season) and two intrinsic (age and sex) factors in explaining the prevalence of, and variation in worm burdens of, *H. p. polygyrus* among wood mice from three contrasting habitats in the UK. We were unable to evaluate the contribution of host age in the full statistical models because of some missing data subsets but it can be seen readily from the summary statistics in figs 1 and 2 that, as expected and consistent with other studies (Elton *et al.*, 1931; Gregory, 1992; Gregory *et al.*, 1992), juvenile mice generally harboured lower worm burdens than adults. Perhaps surprisingly, the second intrinsic factor, host sex, contributed little to the models other than through interactions with site and season, arising from the male bias in worm burdens at the Isle of Wight and a female bias at the other two sites. In this respect our data are consistent with those of Gregory (1991, 1992) who similarly found no sex difference in intensity of infection with *H. polygyrus* but differ from other studies reporting significant sex differences (Lewis, 1968; Lewis & Twigg, 1972). It may be pertinent that few published studies have taken into consideration a range of factors affecting worm burdens and rigorously evaluated the sex effect in context.

In our study, the two extrinsic factors (season and site) were the principal determinants of variation in worm burdens among adult mice and their relative contribution (see table 3, as adjudged by the change in deviance) was about equal. Moreover, the interaction between site and season was the strongest of the significant interactions indicating that seasons affected worm burdens in different ways among the three sites. Seasonal variations in worm burden *per se* are not unexpected, since earlier studies have well documented fluctuations in the intensity of infection with *H. polygyrus* across seasons in various locations in the UK. However, the contribution of site and the seasonal influence on the site effect (the interaction between season and site) were both less expected and deserve some explanation.

It is evident from fig. 2 that it is the Dungeness site which contrasts with the other two, Egham and Isle of Wight showing broadly similar patterns to each other. In both of the latter two sites a clear depression in worm burdens was apparent in the autumn, when presumably young mice entered the adult cohorts but had not yet acquired heavy worm burdens. Highest worm burdens were detected, much as expected, in the winter and spring. In contrast at Dungeness, not only were the prevalence and intensity of infection lower, but the seasonal pattern was quite distinct from that recorded at Egham and the Isle of Wight. High worm burdens were only detected in the spring, and mice carried generally low worm burdens right across the remaining three seasons, suggesting that throughout summer, autumn and winter conditions were not conducive for transmission.

At this stage we cannot exclude the possibility that adult worm mortality was higher and hence life span shorter during the summer–winter period, but the more likely explanation is that acidification of the soil surface at Dungeness (Ferry & Waters, 1988) contributed to a higher mortality of the free-living transmission stages compared with the other sites. Transmission of *H. polygyrus* entails deposition of eggs in host faeces and three free-living larval stages which feed on faecal bacteria whilst developing into the infective L3 stage (Fahmy, 1956; Bryant, 1973), a phase during which they are sensitive to environmental stressors. Abu-Madi (1994) showed that under laboratory conditions the mortality of L3 stages of *H. polygyrus* increased at pH values of 4 and 5 compared with pH 7. Therefore, the physical features, including soil structure, moisture, temperature, pH and vegetation of the Dungeness site may have been unsuitable for optimal development of the free-living component of the life

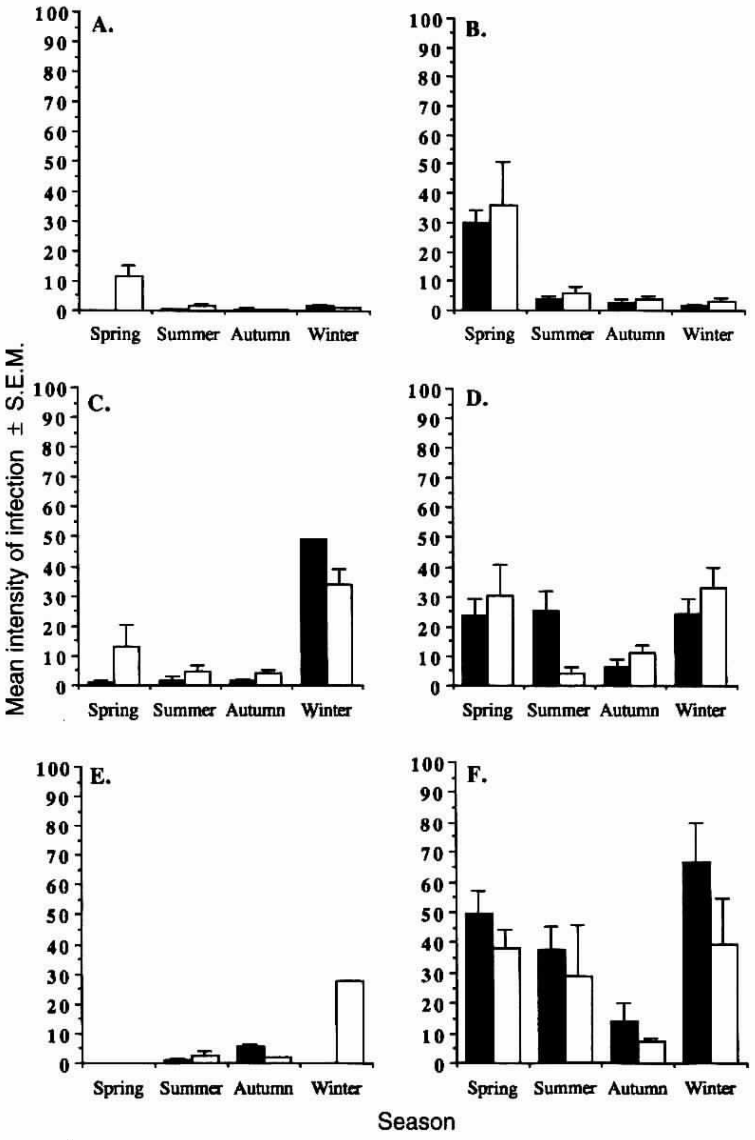

Fig. 2. Seasonal variation in the intensity of infection with *Heligmosomoides p. polygyrus* in *Apodemus sylvaticus* across three habitats (A and B, Dungeness; C and D, Egham; E and F, Isle of Wight) and by host age (juveniles A, C and E; adults B, D and F) and host sex (males filled in columns, females open columns).

cycle, thereby reducing the rate of transmission by greater mortality of larvae compared with the other two sites (Kerboeuf, 1978).

The mice trapped at Dungeness were also obtained from a thin band of vegetation (approximately 20–50 m wide) around the edge of Open Pits 1 and 2, which was isolated and surrounded by extensive margins of shingle. Small rodents are unlikely to readily risk entering exposed wide tracts of shingle, particularly since potential nocturnal predators may be alerted by noise arising from movements over the shingle substratum (J. Hurst, *personal communication*). Therefore, it is possible that the rodent communities associated with specific pits were isolated from surrounding populations creating an opportunity for genetic drift in a variety of host characteristics including innate and acquired immunity, behaviour and social organization, any of which may have affected the overall pattern of infection by reducing recruitment of new larvae into the adult worm population (resistance to establishment) and shortening adult worm life span (anti-adult worm resistance).

By employing log-linear analysis, we have been able to evaluate accurately the contribution of both extrinsic and intrinsic factors (excepting age) in influencing the parasite burdens of wild populations of mice. Our study has raised several pertinent questions, not the

least of which is the intriguing difference in the manner in which seasonal fluctuations in parasite burdens operated across our three study sites. The unusual characteristics of the Dungeness site warrant further investigation.

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